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# Friend or foe? Large canid remains from Pavlovian sites and their archaeozoological context

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ABSTRACT

In this paper we discuss recent claims that dogs were first domesticated from wild wolves in the Middle Upper Paleolithic (MUP), about 27 ka BP. According to our data, we think the presence of large canids at the Pavlovian/MUP sites is a result of hunting specialization and not a sign of an early process of dog domestication. Our interpretation is supported by the following observations, whose implications we discuss: (1) Pavlovian faunal assemblages from seven sites in Moravia contain relatively high numbers of large canids; (2) gnaw-marking by large canids occurs with low frequency on the animal bones in these assemblages; (3) the bones of Pavlovian large canids in the sites often have cut marks from skinning, dismembering, and filleting. Whatever the reasons MUP people had for killing wolves, such as for food or for the skins, the effect would have reduced competition for prey between humans and wolves. The relatively high frequency of wolves at Pavlovian sites may have been a side effect of settlement aggregation and long-term occupations of sites, which could have attracted wolves to the settlements, and thus increased the need for humans to reduce their numbers.

## 1. Introduction

The question of the earliest domestication of dogs is an important one in current debates about the evolution of human societies, not only because the dog was the first domesticated animal species, but also because of this species' strong relation with humans and its adaptability that enabled rapid spread over most of the world (Vilà et al., 1997; Clutton-Brock, 1995; Wang and Tedford, 2008; Crockford, 2000; Olsen, 1985). A determination of the place(s) and time(s) of this major event will allow a better understanding of Paleolithic ecology and community processes.

It is generally agreed that dogs had been domesticated by the Late Glacial, as based on archeology (Clutton-Brock, 1995; Morel and Müller, 1997; Musil, 2000; Morey, 2010; Napierala and Uerpmann, 2010; Pionnier-Capitan et al., 2011; Boudadi-Maligne et al., 2012) and paleogenetic studies (Botigué et al., 2017; Deguilloux et al., 2009; Kim et al., 1998; Leonard et al., 2002; Laurent et al., 2016; Lindblad-Toh et al., 2005; Savolainen et al., 2002; Vilà et al., 1997; Vonholdt et al., 2010). Recently the possibility of even earlier domestication has gained pace from new interpretations of the Middle Upper Paleolithic (MUP) faunal record (Germonpré et al., 2012, 2013, 2015, 2017, 2018). Several recent publications propose dogs were first domesticated from wolves in southern Moravia before the Last Glacial Maximum, about 27 ka BP. This proposal mainly arose from a suggestion that large canid remains excavated at the Pavlovian site Předmostí are from domesticated dog (Germonpré et al., 2012). Publications have since appeared which attempt to explain the relationships between humans and large canids during the Gravettian and Epigravettian Upper Paleolithic period, and new announcements have been made of Paleolithic dogs, often from archeological sites in the Russian Plain (Sablin and Khlopachev, 2002; Ovodov et al., 2011; Shipman, 2015a,b; Bocherens et al., 2015; Nikolskiy and Sotnikova, 2018).

We think those claims are not sufficiently proved. Our conclusion is based on archaeozoological studies of mammalian bones from the Moravian sites of Pavlov I Southeast (SE), Pavlov II, Pavlov VI, Dolní Věstonice I, Dolní Věstonice II, Milovice IV, and Předmostí. Faunal assemblages from these sites contain numerous remains of large canids, accounting for over 1/4 of all identified animal remains (Svoboda et al.,

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2011; Wojtal et al., 2012, 2018, 2020; Wilczyński et al., 2015a). In addition to relying on descriptions that have already been published, we carried out osteometric analysis of large canid mandibles, the skull part that was most often best preserved, and isolated teeth.

On the basis of our studies, we join the debate about the possible first domestication of dogs from Pleistocene wolves and its consequences for MUP or earlier human populations (Crockford and Kuzmin, 2012; Germonpré et al., 2009, 2012, 2015, 2017; Germonpré and Sablin, 2017; Shipman, 2015a,b; Bocherens et al., 2015; Morey, 2014).

## 2. Material and methods

The animal bones and teeth discovered at the seven Pavlovian mega-sites named above are stored in Budisov Castle of the Moravian Museum (Moravské zemské muzeum) and at the Dolní Věstonice Research Centre of the Institute of Archaeology, Czech Academy of Science. We examined the stored bone materials which had been excavated at the Moravian sites Pavlov I SE (Klíma excavation) and Dolní Věstonice I and II (Czech Republic, Absolon, Klíma, and Svoboda excavations), and collated data from other sites mentioned above. A complete archaeozoological analysis of Předmostí I was not carried out because information about traces made on bones by humans or carnivores and counts of mammoth remains and individuals have not been made, and many animal remains were not available to study. However, published data (Pokorný, 1951) indicate that with the exception of the mammoth data the Předmostí faunal assemblage does not differ significantly from the data we obtained for other Pavlovian mega-sites. Similar data was obtained for the material recently discovered during excavations in Předmostí led by J. Svoboda in 2006 (Wojtal and Wilczyński, 2013).

Frequencies of skeletal elements and animal individuals were measured in terms of the Number of Identified Specimens (NISP) and Minimal Number of Individuals (MNI). NISP is defined as the number of specimens identified to taxon in a collection. MNI was estimated by sorting but not matching left and right elements. Also calculated were MNE and MAU values. MNE (Minimal Number of skeletal Elements) is an estimation of the number of skeletal elements represented by specimens in the assemblage, based on the most common portion of the element considered (Klein and Cruz-Uribe, 1984; Lyman, 1994). MAU (Minimal number of Animal Units) was calculated by dividing MNE of each skeletal element by the number of that element in a living animal. The MAU values were standardized by dividing MAU value of each element by the highest MAU value in the skeletal collection of each taxon and multiplying by 100 to produce % MAU, which is comparable to percentage survivorship of skeletal elements (Lyman, 1994; Lyman, 2008).

Here we use the term “large canid” when referring to wolf-sized canids, instead of wolf, to avoid bias in our descriptions. In the large canid material a wide morphological diversity is visible, both in the cranial and post-cranial skeleton (Fig. 1). Recent studies of large canid remains from Dolní Věstonice II suggest that hunters from that site probably had access to multiple wolf ecomorphs, both geographically and chronologically (Perri and Sázelová, 2016). Similar conclusions were obtained for materials from Předmostí where specimens are normally varying (Janssens et al., 2019).

For the large canid remains from Pavlov I SE and Dolní Věstonice I, we calculated ages of individuals on the basis of wear on the lower first molar (Gipson et al., 2000), including isolated specimens and those still rooted in mandibles. Mandibular incisors were not available for examination of wear in the Pavlovian site assemblages. Wear was examined on right and left molars, and both determinations were recorded. The data were used to make age profiles (a.k.a. mortality profiles). This analysis was done to compare the age profile of large canids from these sites to the age structures of recent wild wolves, as a way to estimate possible selectivity in killing, such as by human actions.

All bones were examined closely to document traces left by human and animal activities and the abiotic environment. All bone modifications were noted except for root etching, which generally occurred on most bones. The bones from the studied sites were closely examined to identify cut marks using criteria established by several authors (e.g., Shipman and Rose, 1983; Olsen and Shipman, 1988; Lyman, 1994; Domínguez-Rodrigo et al., 2009), such as their location on bones and features such as cross-sectional shapes. The locations of cut marks reflect different steps in human processing of animal carcasses (Binford, 1981; Lyman, 1994). To check if there are differences in the proportion of the bones with cut marks the Generalized Linear Model with binominal distribution and logit function was used TIBCO Software Inc. (2017).

Other human-made modifications sought on the bone material were traces of fire. Humans burn bones intentionally, such as when used as fuel in fires for cooking animal parts or to warm themselves, or for disposing of refuse. Bone are also burned through unintentional exposure to man-made or natural fires (Stiner et al., 1995; Théry-Parisot, 2002; Villa et al., 2002).

Bones from the sites were also examined for carnivore modifications. Carnivores are important taphonomic agents affecting bone preservation, potentially influencing bone survival and representation in the assemblage. Characteristic types of damage caused by carnivores have been described by Binford (1981), Haynes (1980, 1983a), and Lyman (1994), among others, who have noted different modifications such as tooth punctures, pits, scores, and furrows. The dimensions and shapes of tooth marks sometimes allow identification of the taxon responsible for gnawing (Haynes, 1983a; Domínguez-Rodrigo and Piqueras, 2003; Sala et al., 2014). Bones were also examined to find rodent gnaw marks, which are closely spaced and parallel flat-bottomed grooves (Lyman, 1994).

## 3. Results

### 3.1. Archaeozoological analysis of Pavlovian bone assemblages

Animal bone assemblages at Pavlovian sites are among the most abundant known from European open-air Paleolithic sites (Absolon, 1945; Klíma, 1963, 1990; Musil 2010; Wojtal et al., 2012, 2018, 2020; Wilczyński et al., 2015a). In the Pavlovian assemblages we studied > 80,000 remains from 18 different species (Table 1). The most numerous remains were bones and teeth of mammoth, horse, reindeer, and carnivores. The proportion of large canid (wolf sized), wolverine, and foxes (red and Arctic fox) is high, and in all cases comprise ~1/3rd of the assemblages (Wojtal et al., 2012, 2018, 2020; Wilczyński et al., 2015a). Such a high proportion of carnivores at Pavlovian sites is typical, and is seen at sites throughout central Europe, even in localities where excavations were limited in area (Fladerer, 2001; Svoboda et al., 2011; Wojtal et al., 2011; Wilczyński et al., 2017). The large proportion of carnivores significantly decreases at Late Gravettian localities, where mammoths or reindeer prevail (Lipecki and Wojtal, 1998; Wojtal and Sobczyk, 2005; Brugère and Fontana, 2009; Vlačiky, 2009; Wilczyński et al., 2012, 2015b).

At Pavlovian sites the frequency of large canid remains is always high, and varies from 12.5% at Dolní Věstonice II to ~23% at Dolní Věstonice I and Pavlov I SE. The large canid MNI ranges from 11.3% at Dolní Věstonice II to 22% at Dolní Věstonice I. These proportions are comparable to the MNI range of similarly sized reindeer, which was undoubtedly hunted for human subsistence (Table 1). Comparison of the frequencies of individual skeletal parts (%MAU) of these two animals shows similarities, although some body parts are differentially abundant for large canids and reindeer (Table 2). The most visible differences are the significantly higher share of mandibles, first cervical vertebrae (atlas), and upper forelimbs (scapulae and humerus) of large canids in comparison to reindeer. The differences might be explained by taphonomic/excavation processes or unusual human selectivity. Even

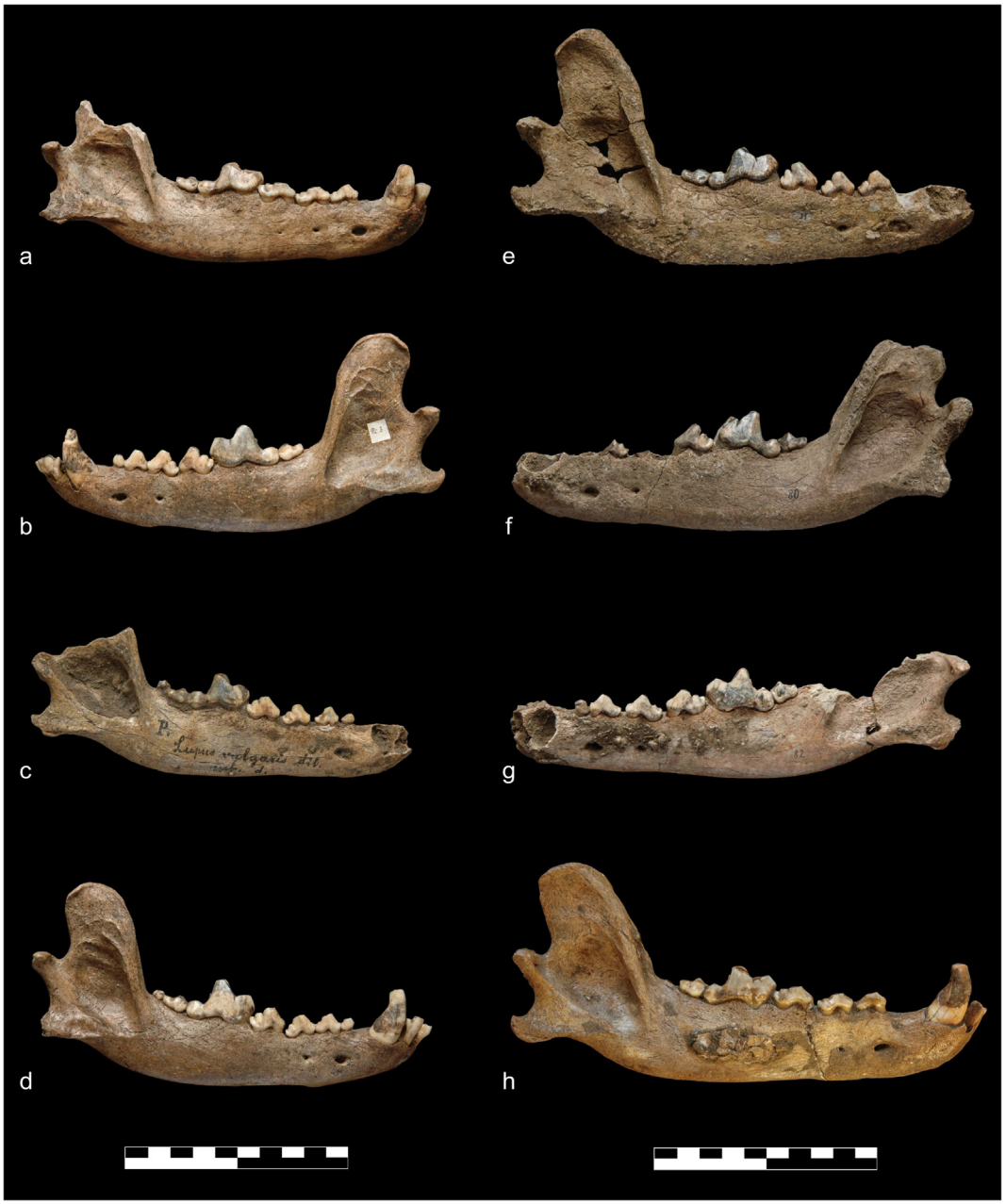


**Fig. 1.** Dolní Věstonice II and Pavlov I SE site - variability in large canid hemimandibles.

so, the similar proportions of most body parts suggest that whole carcasses of both large canids and reindeer were transported to all the Pavlovian sites we have analyzed (Fig. 2).

For Pavlov I SE, animal ages were determined from 56 teeth of large canids (33 right and 23 left lower first molars). For Dolní Věstonice I, 38 ages were determined (24 right and 14 left lower first molars). At both sites the best represented individuals are < 3 years old (cusps on carnassials are without traces of wear), representing ~40% of all large canids in the assemblages (Table 3). The progressively older age classes from Pavlov I SE have decreasing proportions. The best represented are youngest animals, and few individuals represent the oldest age classes. We note the presence of very old (> 10 years old) individuals with heavily worn teeth. We also point out that all individuals in the youngest age category in this table, < 3 years, had all permanent teeth erupted without visible wear, and no individuals were found with deciduous teeth. No skeletal remains of pups or juveniles have been identified in the Pavlovian localities we studied.

Age structure varies in recently studied wild wolf packs, often due to human hunting pressure (Gude et al. 2012). The percentage of immature wolves (< 1 year old) varies from 13% in populations which are unexploited by humans, to as high as 55% in exploited populations (references in Mech, 1970: 354–359). There are no immature large canids < 1 year old in the Pavlov I SE assemblage, but otherwise the age profile is similar to the general pattern in recent free-living wolf populations in which individuals < 3–4 years of age predominate (Mech, 1999). A similar pattern occurs in assemblages from Neolithic archeological sites: young and subadult animals are relatively the most abundant (Pionnier-Capitan, 2010). Results obtained for Dolní Věstonice I are distinct from the Pavlov I SE results, because of the higher share of large canids 4–8 years old. If the large canids were wild wolves, most individuals that old would have dispersed from their natal packs and started their own packs which would be numerically dominated by recent offspring < 3–4 years old. The high proportion of prime-age adult large canids at Dolní Věstonice I might be related to selective

**Table 1**
NISP (Number of Identified Specimens), and MNI (Minimal Number of Individuals) of mammals from Dolní Věstonice I (DV I), Dolní Věstonice II (DV II), and Pavlov I SE.

| Taxon | DV I | | DV II | | Pavlov I SE | |
|---|---|---|---|---|---|---|
| | NISP | MNI | NISP | MNI | NISP | MNI |
| *Castor fiber* (European beaver) | – | – | 2 | 1 | 9 | 2 |
| *Lepus* sp. (hare) | 288 | 5 | 1714 | 60 | 6773 | 192 |
| *Gulo gulo* (wolverine) | 381 | 8 | 150 | 8 | 781 | 10 |
| *Lynx lynx* (lynx) | 1 | 1 | 2 | 1 | – | – |
| *Panthera spelaea* (cave lion) | 18 | 1 | 5 | 1 | 81 | 3 |
| *Vulpes lagopus/ Vulpes vulpes* (Arctic/red fox) | 766 | 52 | 1122 | 51 | 5460 | 123 |
| ***Large canid (Canis lupus*-sized)** | **1641** | **33** | **913** | **20** | **6190** | **57** |
| *Ursus* sp. (bear) | 51 | 2 | 40 | 2 | 50 | 4 |
| *Ursus* sp./*Panthera spelaea* (bear/ cave lion) | 25 | – | – | – | 165 | – |
| *Equus ferus* (horse) | 752 | 8 | 110 | 5 | 589 | 10 |
| *Mammuthus primigenius* (woolly mammoth) | 1959 | 17 | 2439 | 5 | 2264 | 7 |
| *Coelodonta antiquitatis* (woolly rhinoceros) | 5 | 1 | – | – | 2 | 1 |
| *Megaloceros giganteus* (giant deer) | – | – | 5 | 1 | – | – |
| *Alces alces* (European elk) | 1 | 1 | – | – | – | – |
| *Cervus elaphus* (red deer) | 2 | 1 | – | – | 4 | 1 |
| *Capra ibex* (Alpine ibex) | – | – | – | – | 5 | 1 |
| ***Rangifer tarandus* (reindeer)** | **941** | **18** | **783** | **20** | **4517** | **56** |
| *Bos primigenius/Bison priscus* (aurochs/steppe wisent) | 10 | 1 | 3 | 1 | 3 | 1 |
| Total of identifiable bones | **6841** | **149** | **7288** | **176** | **26,893** | **467** |
| Small mammal (fox-hare sized) | 266 | – | 362 | – | 4701 | |
| Medium mammal (reindeer-wolf sized) | 411 | – | 1152 | – | 1954 | |
| Large mammal (horse-bear sized) | 350 | – | 124 | – | 555 | |
| Very large mammal (mammoth sized) | 1358 | – | – | – | 616 | |
| Mammalian indeterminate | 1193 | – | 16,350 | – | 11,747 | |
| **Total** | **10,419** | **149** | **25,276** | **176** | **46,466** | **467** |

**Table 2**
%MAU (Minimal Animal Units) of large canids and reindeer from Dolní Věstonice I (DV I), Dolní Věstonice II (DV II), and Pavlov I SE.

| | Pavlov I SE Reindeer %MAU | Pavlov I SE Large canid % MAU | DV I Reindeer %MAU | DV I Large canid % MAU | DV II Reindeer %MAU | DV II Large canid % MAU |
|---|---|---|---|---|---|---|
| Cranium | 43.4 | 33.9 | 28.2 | 40 | 30.3 | 26.3 |
| Mandible | 49 | 60.7 | 19.8 | 40 | 15.2 | 100 |
| Atlas | 25.2 | 91.1 | 11.1 | 76.9 | 24.2 | 84.2 |
| Axis | 37.8 | 91.1 | 22.2 | 30.8 | 66.7 | 68.4 |
| Vertebrae | 16.5 | 35 | 16.9 | 7.7 | 7.2 | 8.1 |
| Scapula | 41.4 | 64.3 | 38.9 | 23.1 | 24.2 | 71.1 |
| Humerus | 56.8 | 69.6 | 55.6 | 98.5 | 42.4 | 76.3 |
| Radius | 77.5 | 61.6 | 63.9 | 63.1 | 63.6 | 55.3 |
| Ulna | 70.3 | 59.8 | 25 | 100 | 100 | 68.4 |
| Carpals | 50 | 42.3 | 28.2 | 13.4 | 28.8 | 10.5 |
| Metacarpals | 41.4 | 69.5 | 13.9 | 35.7 | 48.5 | 41.1 |
| Innominate | 10.8 | 47.3 | 5.6 | 13.8 | 27.3 | 21.1 |
| Femur | 15.3 | 36.6 | 11.1 | 26.2 | 15.2 | 13.2 |
| Tibia | 100 | 57.1 | 63.9 | 44.6 | 66.7 | 42.1 |
| Fibula/Os malleolare | 41.4 | 17 | 11.1 | 1.5 | 24.2 | 7.9 |
| Calcaneus | 73 | 100 | 72.2 | 73.8 | 78.8 | 57.9 |
| Astragalus | 94.6 | 76.8 | 100 | 35.4 | 66.7 | 52.6 |
| Tarsals | 39.6 | 58.9 | 44.4 | 17.8 | 31.8 | 14.7 |
| Metatarsals | 39.6 | 75.9 | 44.4 | 28.5 | 36.4 | 42.8 |
| Phalanx | 19.8 | 51.3 | 22.2 | 15.9 | 13 | 11.1 |

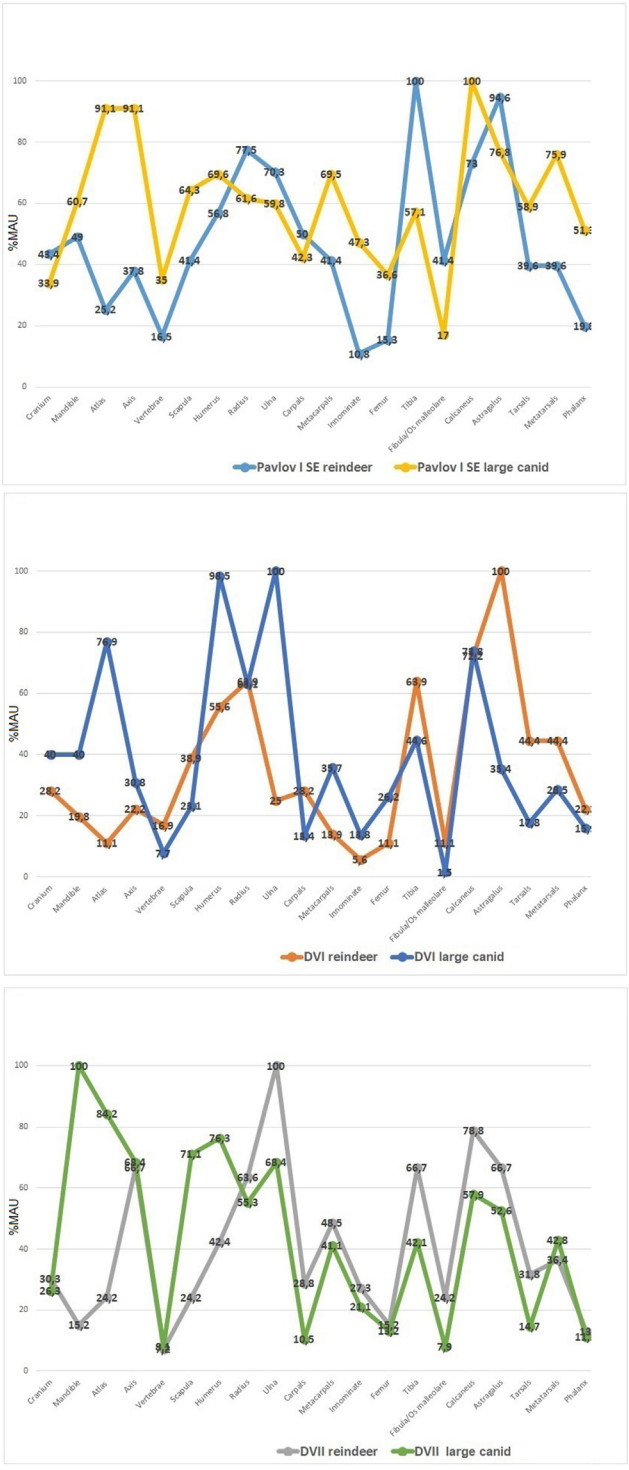


**Fig. 2.** Graph illustrating %MAU (Minimal Animal Units) of large canids and reindeer from Dolní Věstonice I (DV I), Dolní Věstonice II (DV II), and Pavlov I SE.

human hunting for largest animals.

### 3.2. Human activity affecting large canid and reindeer bones

Numerous cut marks were noted on large canid and reindeer remains, related to different human actions, which is seen on up to 2.3% of the wolf-sized large canid remains in the case of Dolní Věstonice I (Table 4). The type and frequency of cut marks on large canid bones are

**Table 3**
Age structure of large canids discovered at Dolní Věstonice I and Pavlov I SE site.

| Age in years | Dolní Věstonice I | | | | Pavlov I SE | | | |
|---|---|---|---|---|---|---|---|---|
| | Right | % | Left | % | Right | % | Left | % |
| < 3 | 10 | 41.67 | 2 | 14.29 | 13 | 39.39 | 6 | 26.09 |
| 3–4 | 1 | 4.17 | 2 | 14.29 | 8 | 24.24 | 6 | 26.09 |
| 4–6 | 8 | 33.33 | 4 | 28.57 | 7 | 21.21 | 5 | 21.74 |
| 6–8 | 2 | 8.33 | 6 | 42.86 | 3 | 9.09 | 3 | 13.04 |
| 8–10 | 3 | 12.5 | – | – | 1 | 3.03 | 1 | 4.35 |
| 10–12 | – | – | – | – | 1 | 3.03 | 2 | 8.7 |
| | 24 | 100% | 14 | 100% | 33 | 100% | 23 | 100% |

less numerous than on reindeer bones but reflect analogous human actions. At the same time, traces of cutting visible on the remains of wolf-sized large canids are the most numerous compared to the remains of other predators from the analyzed sites (Wojtal et al., 2020). The cuts are mostly related to the dismembering of carcasses and rarely to skinning or filleting. It should be noted that such cut marks are also noted on the remains of other carnivore species such as wolverine, foxes, cave lion, and bear (Wojtal et al., 2012, 2018, 2020; Wilczyński et al., 2015a).

Statistical analysis shows that reindeer bones bear proportionally more cut marks than those of large canids (Wald $\chi^2 = 40.34$; $p < 0.000001$) and each site also differs in the number (frequency) of cut marks (Wald $\chi^2 = 29.52$; $p < 0.000001$). The largest proportion of cut marks on bones is observed at Dolní Věstonice I, while Dolní Věstonice II and Pavlov I SE have similar proportions that are lower than the proportion from Dolní Věstonice I. There is also appreciable interaction between "species" and sites (Wald $\chi^2 = 17.52$; $p = 0.00016$), where differences among proportions between reindeer and large canids bones with cut marks is much higher at Pavlov I SE than at Dolní Věstonice I and Dolní Věstonice II (Fig. 3). All these differences probably resulted from the intensity of settlement processes occurring at individual sites, but at the same time they also confirm that on Pavlovian sites large canids played a significant role as a prey animal.

Pavlovian people preferred to make tools of mammoth ivory and bones and reindeer antler, while the carnivore teeth were preferred for making pendants. Most often foxes (Arctic fox, red fox) teeth were utilized, but canines and incisors from larger canids were also selected. Of the 351 studied pendants from Pavlov I SE, 65 (18.5%) were made on teeth of large canids. The bones of carnivores, especially long bones, only occasionally were used for manufacturing tools. A similar situation can be seen at other Pavlovian sites, where large canids did not play a special role as a source of raw material for tools, the same as for wolverine or horse (e.g. Klíma, 1963; Svoboda, 2002; Brühl, 2005; Zelinková, 2007). The scarcity of bones from large canids as raw material corresponds to a lack of figurines or other images made to represent large canids in Pavlovian assemblages, generally the case for all

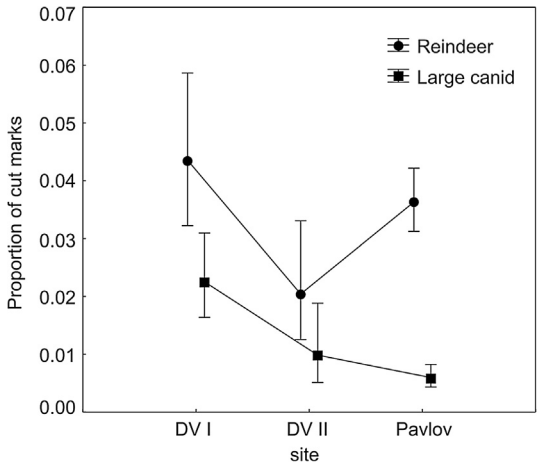


**Fig. 3.** Interaction between "species" and sites on a basis of statistical analysis (95% confidence interval).

Mid Upper Paleolithic art. We think that large canids provided raw material mostly for utilitarian objects, and were targeted for practicality, and not used in symbolic culture.

### 3.3. Results – Carnivore activity

Traces of carnivore activity (gnawing marks) are very rare on Pavlovian site bones. From all examined assemblages we have been able to record few marks, whose dimensions and shapes strongly suggest wolf gnawing (Haynes, 1983a; Fosse et al., 2012; Sala et al., 2014). At Dolní Věstonice I only two bones have clear carnivore gnawing marks, which is 0.02% of the whole bone assemblage (or 0.03% of the sub-assemblage identified to a taxon). The marks are on mammoth bones, namely the distal part of a humerus and a calcaneus. In the Dolní Věstonice II assemblage (total n = 25,547) we found 16 bones with carnivore marks. Gnawing marks are visible on bones of herbivores (mammoth, reindeer) and carnivores (fox, wolverine). Gnawed bones were discovered both at the camp site (n = 8) and at the mammoth bone accumulation (n = 8), and altogether the count is barely 0.06% of the whole assemblage or 0.2% of the remains identified to a taxon. The largest number of carnivore-gnawed bones is from Pavlov I SE (n = 23). Very numerous bones were discovered at this site, but tooth marks have been identified on only 0.05% of the whole material or 0.08% of remains determined to taxon. Most of the gnawed bones belonged to woolly mammoth (n = 8) and reindeer (n = 5). Location and shape of the marks indicate that the marks were probably made by wolves. For example carnivore gnawing marks visible on woolly mammoth bones from Pavlov I SE (Fig. 4a, b) and Kraków Spadzista (Fig. 4c, d) show the same shape and dimensions suggesting that they were left by large canids. Noticeably more intensive carnivore gnawing was seen only on mammoth bones. Single bones of hare, large canid,

**Table 4**
Number of bones with signs of human and carnivore activity discovered at Dolní Věstonice I (DV I), Dolní Věstonice II (DV II), and Pavlov I SE sites.

| Taxon | DV I | | DV II | | Pavlov I SE | |
|---|---|---|---|---|---|---|
| | Reindeer | Large canid | Reindeer | Large canid | Reindeer | Large canid |
| Cut marks – skinning | 2 | 1 | 4 | 3 | 16 | 16 |
| Cut marks – dismembering | 30 | 34 | 11 | 5 | 129 | 16 |
| Cut marks – filleting | 6 | 1 | 1 | 0 | 16 | 3 |
| Cut marks – indeterminate | 3 | 1 | 0 | 1 | 3 | 1 |
| **Cut marks - general** | **41** | **37** | **16** | **9** | **164** | **36** |
| **% of cut marks among reindeer/wolf remains** | **4.6%** | **2.3%** | **2%** | **0.9%** | **3.6%** | **0.6%** |
| Percussion marks | 0 | 0 | 1 | 0 | 9 | 4 |
| Burned bones | 4 | 4 | 1 | 8 | 20 | 21 |
| Gnawing marks | 0 | 0 | 1 | 0 | 5 | 0 |

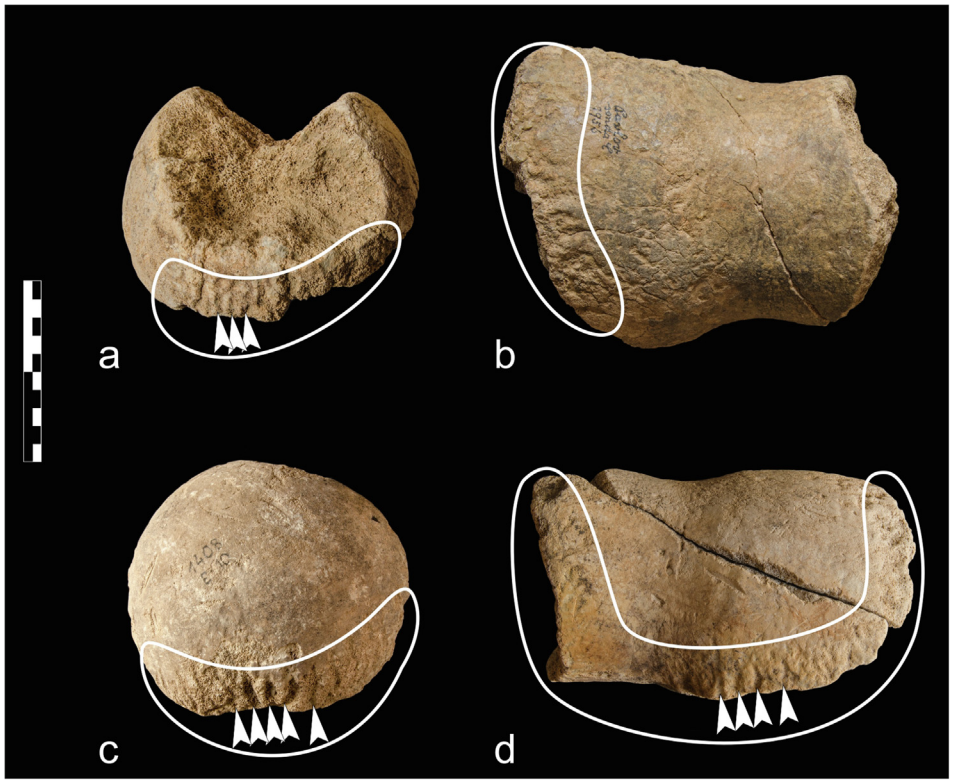


**Fig. 4.** Carnivore gnawing marks identified at Pavlov I SE (a, b) and Kraków Spadzista site (c, d); a and c – femur proximal epiphyses; b and d – humerus distal epiphyses. The gnawing marks are encircled; arrows point to tooth furrows.

and fox were also gnawed, and have only tooth puncture marks.

The low numbers of carnivore gnawing marks and the lack of digested bones and coprolites indicate that large carnivores had strongly limited access to the animal carcasses or carcass parts at Pavlovian sites. During this time in central Europe, the cave hyena already was extinct (Stuart and Lister, 2014), so the wolf would have been the main meat-reliant large carnivore. Reasons why carnivore ravaging was so limited are not apparent, but this feature is relevant to our interpretation that no domesticated dogs were present, as discussed below.

## 4. Discussion

The number of large canid remains at Pavlovian sites certainly hints at an important role this mammal played in MUP societies. Here we discuss this role and speculate about relations between large canids and hunter-gatherers. What we know about large canids at the Pavlovian mega-sites can be summarized thus:

There are relatively large percentages of carnivores in the assemblages;
Only adult large canids are present, without remains of pups or juvenile animals;
The state of preservation of the large canid bones is the same as with other carnivores (foxes, wolverine, bear, lion) — long bones are preserved as a whole or in large fragments, and bones of all body parts have been found;
Bones of large canids bear traces of human actions connected with skinning, dismembering, and meat-removal from carcasses, the same actions that were done with other carnivores and herbivores;
The question of ritual canid burials is still a matter of inverstigation (e.g., the wolf skeleton at Pavlov I, area A (Svoboda et al., 2016), which is in contrast to later periods, such as the Late Paleolithic, Epipaleolithic, Mesolithic, and Early Neolithic, when domestic dogs are known to have been present in Europe;
Bones of large canids were not commonly used for tools, despite their availability. We think this means large canids were seen mainly as sources of meat and hides, and had no special place in human domestic activities;
Carnivore gnawing marks on animal bones are scarce in the Pavlovian assemblages, which indirectly argues for the absence of domesticated dogs. Pavlovian sites were long-term settlements occupied for several seasons. If the people kept dogs, waste from processed animal carcasses would have been available for dogs to feed on, yet there is no evidence for dog-gnawing, especially the extensive kind called a “kennel pattern” which is common where carnivores are attached to human settlements and dependent on provisioning (such as bone waste) for their food (Haynes, 1980: 102–103; Haynes unpubl. field notes 1978–1982). Ethnographically documented human settlements where dogs were kept contain clear evidence of carnivore modifications, such as intense gnawing or removal of body parts (Hudson 1993; Ley-Lara et al. 2015; Ley-Lara and Götz 2016).
Statistical analysis shows that on Pavlovian sites large canids played a significant role as a prey animal.

In 2015 during conference of "European Society for the study of Human Evolution" Germonpré et al. (2018) proposed two hypotheses for an early domestication of dogs: the first is “self-domestication” by wolves, where some individuals scavenged the remains of prey animals left by people at prehistoric human settlements, eventually becoming habituated to human proximity, and the second is “social domestication” in which Upper Paleolithic people actively selected wolf pups in the wild and selectively bred successive generations to produce controllable animals, with accompanying changes in body form such as craniofacial shortening. This second scenario has been proposed to explain specimens of large canids from Předmostí and the Epigravettian Eliseevichi site (Russia).

Our opinion is that neither process is supported by

archaeozoological analysis of MUP sites in central Europe. Recent publications have clearly demonstrated that the process of dog domestication cannot be unambiguously detected merely by noting some morphological differences in bones of large canids at a few early archaeological sites (Drake et al., 2015; Janssens et al., 2019).

At sites where domesticated dogs were unquestionably present, several features can be noted that reflect their presence. The most apparent is a low number of dog remains. Dog remains discovered from Neolithic, Bronze Age, and later periods of Europe occur relatively sporadically in assemblages, and the percentage usually does not exceed 4% of faunal remains (e.g., De Grossi Mazzorin and Tagliacozzo, 1997; Albarella et al., 2017; Bökönyi, 1983; Benecke, 1994, Kovačiková et al., 2012), although with extraordinary exceptions (Abogast, 2016; Zeeb-Lanz et al., 2009). At prehistoric Inuit sites dog remains are always meager; for example at the Early Thule Cache Point site dog remains were 1.7% of the total NISP and 4.9% of the total MNI (Friesen and Betts, 2006). Secondly, at sites were domesticated dogs were present, relatively numerous bones with gnawing marks have been recorded. This could be observed from the early Neolithic settlements in Europe till recent times; at all settlements which contain post-consumption deposits the proportion of gnawed bones generally ranges from 2% up to 10%. At Holocene Inuit sites the proportion of gnaw-marked bones varied from 1% to around 20% (Binford, 1978; Friesen and Betts, 2006; Meldgaard, 2004). The third feature is occurrence of intentional dog burials, sometimes interred together with human in grave-pits, which has led to conclusions that dogs played an important – and symbolic – role among hunter-gatherer and farming populations. Such cultural behavior is firstly observed at Final Paleolithic Natufian sites as well as in the Mesolithic/early Holocene, (e.g., Bate 1937; Dayan 1994; Tchernov and Valla 1997; Davis and Valla 1978; Grünberg 2013; Morey and Wiant 1992; Radovanović 1999,; Raisor 2005). Intentional dog burials are widely recorded in the later periods (Albarella et al., 2017; Harcourt 1974; Horard-Herbin et al., 2014; Zeeb-Lanz et al., 2009). And fourthly, Prehistoric sites with unquestioned domesticated dogs usually contain little (or no) evidence of the skinning, filleting, and dismembering of dogs, (Harcourt 1974; Horard-Herbin et al., 2014; Mannermaa et al., 2014).

All four features mentioned above positively differ from the data obtained from Pavlovian sites, which have no large canids in burials but which have many bones of large canids in camps. The Inuit site assemblages may be the most relevant of our comparative samples, because of similar paleoenvironmental conditions and a similar economy reliant on hunted animals. The data collected from those sites differ significantly from what is discovered in Pavlovian sites. The Pavlovian sites have a scarcity of gnawing marks on mammal bones but contain a significant share of large canid remains in the assemblages. We acknowledge that the scarcity of gnawing marks in Pavlovian assemblages might have been due to people preventing large canids from having access to animal carcass parts. Hunter-gatherers may not have allowed the large canids to consume as much human-acquired food as the Inuit dogs, especially if the large canids in the Pavlovian settlements were not put to hard work such as sled-hauling. Even so, it is very likely that if the Pavlovian large canids were dogs and not wild wolves, they had to be provisioned with food, and a significant proportion of the faunal materials at early sites expectably should be canid-gnawed. And finally, we note that at all Pavlovian assemblages the data clearly indicate that large canids were butchered and consumed by hunter-gatherers. The examples we have cited show that at the sites where domesticated dogs were known to be present, their representation in the faunal material is low (rarely $>$ 2%), but the frequencies of gnawed bones in the assemblages are relatively high, which is very unlike the patterns in Pavlovian faunal materials.

We acknowledge that Pavlovian hunter-gatherers had a complex relationship with Pleistocene large canids that we conclude were wolves, attested by the large number of remains of this taxon and the presence of almost complete or articulated fragments of wolf-sized body parts. We also note that bones of lion and wolverine were similarly treated in Pavlovian assemblages (Klíma 1976; Svoboda, 2005; Svoboda et al., 2016), and these species were never domesticated.

## 5. General comments on the claims for early domesticated dogs

Large canid materials from cave sites (Goyet Cave, Belgium, and Razboinichya Cave, Siberia) without stratigraphical context have been classified as early examples of domesticated dogs (Germonpré et al., 2009; Ovodov et al. 2011). We agree with Crockford and Kuzmin (2012) that these claims are premature and unwarranted. Our disagreement is based on several critical issues which we have identified from Předmostí.

According to an isotopic study (Bocherens et al., 2015), humans living at Předmostí did not consume reindeer meat and mainly consumed mammoth. Another isotopic study of large canids from Předmostí (Bocherens et al. 2019) has shown a clear dietary difference between the larger Pleistocene forms of large canids (high in mammoth meat) and the smaller forms of large canids (high in reindeer meat), which has been interpreted to mean the smaller canids were domesticates whose dietary regime was under strict human control. The suggestion of dietary control arose from historical or modern ethnoarchaeological examples of hunter-gatherers tying up their working dogs to prevent access to selected food stores (Bogoras 1904; Spencer 1959; Abe 2005), consisting mainly of meat and bones from medium size ungulates. The canids thought to be domesticated dogs at Předmostí therefore were interpreted as having a diet which was the opposite of the human diet at the site – they ate mostly reindeer, while humans ate mostly mammoth. We disagree that the isotopic evidence about dietary differences at Předmostí supports the claim of active Gravettian dog-breeding. The immensely greater quantities of bones and meat from mammoth carcasses in Upper Paleolithic sites would have been be so plentiful that feeding the unused parts of mammoth waste to dogs might have been a simple option for MUP people who wanted to keep dogs, and would not have required hunting of another species – reindeer – which was only used to provision dogs. It is difficult to understand how Pavlovian people living so near to discarded mammoth bones could efficiently deny all access to resident domesticated large canids. We think that canid species which were bred and managed by humans would have been allowed to eat the human leftovers, such as the tonnes of unused mammoth bones and viscera, and that humans would not have spent time and energy hunting reindeer only for the purpose of feeding the meat and bones to dogs. Instead, we suggest another explanation for the dietary differences of larger and smaller forms of large canids: the smallest of the site's large canids were morphotypes of wild wolf which preyed on reindeer, and the larger morphotypes were wild wolves which fed on larger prey, namely mammoth. This pattern of correlation between wolf body size and prey body size is documented among recent wild wolf populations; human activity is not necessary to explain dietary differences between wolves of different body sizes. The typical prey preference for modern wild wolves has an upper limit of Size Class IV (large, such as bison, in the designation system of Brain 1981), probably about the size of weaned but still juvenile mammoths. Size Class II and III cervids such as deer and caribou/reindeer are often preferred prey species for wild wolf packs in many ranges, but larger bison and European elk (*Alces alces*) are also preyed upon in northern ranges by wolves of larger body size which hunt in larger packs. We think those variable preferences also were typical of Pleistocene wolves. The fact that reindeer was the mainstay of the smaller large canids at Předmostí and mammoth was primary in the diet of the larger large canids could simply reflect wolf body size and pack size.

The scarcity of gnawing marks at animal assemblages of Pavlovian sites such as Pavlov or Předmostí proves that carnivores did not have access to animal carcasses accumulated at the site, particularly the large deposits of mammoth bones. In recent hunter-gatherer settlements such

as Siberian Inuit communities where dogs were an essential feature of culture as sled-haulers and beasts of burden (Krupnik 1993), the dogs annually consumed 20–35% of the total human-acquired food supply (as estimated in kilocalories), averaging ~28%. More than a quarter of the human-acquired food supply was fed to dogs, consisting not only of meat and soft tissue, but bones too. We conclude that the extent of large-canid gnawing on food bones would be far from negligible in faunal assemblages from sites occupied by people with dogs. This is not the case at Předmostí.

The evidence from the Pavlovian faunal assemblages is consistent with wild wolves rather than dogs being present. Wild wolves unmanaged by humans were hunted by Pavlovian people for their fur, meat, and bones (Wojtal et al., 2012; 2018, 2020), which is why their remains entered the faunal record at human settlements. The bones of Pavlovian large canids bear the traces of skinning, filleting, and dismemberment that unambiguously indicate they were human prey. We do not exclude the additional possibilities that wolves were killed due to the threat they posed to people in the settlements or that they were willingly hunted because they were competitors for Pavlovian hunters; but whatever the reason for humans killing them, they were skinned and probably eaten.

A final point of disagreement is about the speculation that Gravettian human populations kept domesticated large canids to assist in hunting mammoths (Shipman, 2015a). This idea is not supported by archaeozoological analysis of assemblages from sites younger than Předmostí, specifically the Late Gravettian sites Kraków Spadzista and Milovice I, where mammoth remains are extremely plentiful but the remains of large canids are very scarce (Brugère and Fontana, 2009; Wojtal and Sobczyk, 2005; Wilczyński et al., 2012). The share of mammoth remains in the faunas of these two sites is much higher than at the older Pavlovian sites, yet large canid remains are less abundant than at the Pavlovian sites. It seems apparent that dogs were not needed by humans who specialized in hunting mammoths.

## 6. Conclusion

We think the abundance of large canids at the Pavlovian/MUP sites is a result of hunting specialization and is not evidence for an early process of dog domestication. Support for our interpretation comes from osteometric data from other published studies which indicate the Předmostí large canid which is claimed to be a dog is not significantly distinct from the site's other large canids which are recognized as wolves. For example, recently published analyses demonstrate that the large canids in MUP assemblages are not distinct from wolves (Perri 2016; Thalmann and Perri 2018; Janssens et al. 2019). A second point of support is that Pavlovian faunal assemblages have relatively high numbers of large canids but relatively low frequencies of gnaw marking by large canids on animal bones, which is the opposite pattern from Holocene sites known to have domesticated dogs, where there are low numbers of dogs in bone assemblages but relatively high frequencies of carnivore gnawing. Further support is the observation that Pavlovian large canid bones often have cut marks from skinning, dismembering, and filleting, showing that the carcasses were treated the same way as those of reindeer, and the MNIs are similar to those of reindeer; both factors indicating large canids (wild wolves) were treated the same as other prey species. The Pavlovian wolves were trapped or speared for their fur, meat, and bones. The meat might have been eaten in times of game scarcity.

Whatever the reasons for killing wolves, the effect would have reduced competition for prey between humans and wolves. The relatively large frequency of wolves at Pavlovian sites may have been a side effect of settlement aggregation and long-term occupations of sites, which could have attracted scavenging wolves to the settlements, and thus increased the need for humans to reduce wolf numbers. Moreover, in later periods (Late Glacial or in the Holocene) we do not see in the archaeological record such a high ratio of wolf remains, even at Mesolithic or Early Neolithic sites where domesticated dogs are well documented. The Pavlovian sites also do not contain any evidence for humans using large canids in burial practices or other ritual activities, as seen in later sites of the Late Paleolithic, Mesolithic, and Pre-Neolithic/early Neolithic. We think the frequent appearance of wolves in such high numbers during the Pavlovian period was an exceptional situation, which did not affect the subsequent relations of humans with this predator, as evidenced by the near disappearance of wolf remains from Late Gravettian localities that have large accumulations of mammoth bones, such as Kraków Spadzista and Milovice I.

At the end we would like to emphasize that in order to reconstruct the process of domestication, we must not consider only single findings from one or two sites or rely only on limited kinds of data such as morphology or osteometrics. The search for the evidence of earliest dog domestication must take into account all available factors, particularly archaeozoological data as we have suggested in this paper. A broader analysis would examine contexts, behaviors, isotopic paleoecology, taphonomy, and archaezoological data in order to approach reliable reconstructions of human lifeways and changing relationships with animal communities.

## CRediT authorship contribution statement

**Jarosław Wilczyński:** Investigation, Writing - original draft, Methodology, Writing - review & editing, Supervision, Project administration, Funding acquisition. **Gary Haynes:** Methodology, Writing - review & editing. **Łukasz Sobczyk:** Software, Visualization. **Jiří Svoboda:** Resources. **Martina Roblíčková:** Resources. **Piotr Wojtal:** Investigation, Data curation, Visualization, Writing - review & editing, Funding acquisition.

## Declaration of Competing Interest

The authors declared that there is no conflict of interest.

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## Appendix A. Supplementary material

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